

ECHINASTER GRAMINICOLA. A NEW SPECIES OF
SPINULOSID SEA STAR
(ECHINODERMATA: ASTEROIDEA) FROM THE
WEST COAST OF FLORIDA

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Abstract.—A new species of the sea-star genus *Echinaster* is described from shallow-water seagrass and oyster beds of the west coast of Florida. The new species and *E. spinulosus* Verrill are sibling species, morphologically distinguished only by spination and differences in the secondary skeleton. The two species also differ in coloration and in many physiological, reproductive, and ecological characteristics.

On the west coast of Florida, there are two shallow-water forms of *Echinaster* which conform to Downey's (1973) description of *E. modestus* Perrier, 1881. Prior to Downey's monograph of sea stars of the Caribbean Sea and Gulf of Mexico, authors called both forms *E. echinophorus* or *E. spinulosus* (see Ferguson 1975a). Until recently (Campbell and Turner 1979), the morphological differences between the two forms were unknown (Ferguson 1976). Our recent examination of the type specimens of *E. modestus* has shown that neither form belongs to this species (Turner and Campbell 1981).

Turner and Lawrence (1979) used the terms "light" and "dark" to describe the two forms based on reliable differences in color of the integument of live animals. These morphs have also been called "Type I" and "Type II," respectively, by Atwood (1973a) and subsequent workers. In addition to coloration, the two forms differ in larval development (Atwood 1973a) and environmental tolerances (Watts *et al.* 1982), other life-history parameters (Scheibling 1982; Scheibling and Lawrence 1982), fatty-acid profiles (Ferguson 1976), physical and chemical properties of their eggs (Turner and Lawrence 1979), habitat (Campbell 1978), and diet (Scheibling 1982). Ferguson (1976), Turner and Lawrence (1979), and Watts *et al.* (1982) suggested that the two forms might be different species. We have positively identified the light form (Type I) as *Echinaster spinulosus* Verrill, 1869, by comparison with Verrill's type-specimens at the Peabody Museum. The dark form (Type II) is herein described as a new species, types of which are deposited in: U.S. National Museum of Natural History, Smithsonian Institution (USNM); Museum of Comparative Zoology, Harvard University (MCZ); Peabody Museum of Natural History, Yale University (YPM); Marine Research Laboratory, Florida Department of Natural Resources (DNR FSBC); British Museum (Natural History) (BMNH).

Family Echinasteridae Verrill, 1867
Echinaster Müller and Troschel, 1840
Echinaster graminicola, new species
Figs. 1-3

Diagnosis.—Small. Rays 5, tapered. Madreporite circular, with convoluted gyri; peripheral spinules often present, few; gyal spinules usually absent or few. Serial

ossicles of rays: carinals (sometimes separated by intercalary ossicles), adradials, 1 row of dorsolaterals, superomarginals, long row of intermarginals, inferomarginals, adambulacrals; all series except proximal superomarginals with distal imbrication; patches of glassy tubercles well developed; spines small, conical, subacute, and generally 0–1 per ossicle except for adambulacrals (2–4, of which only 1 is a furrow spine). Actinolaterals absent. Each mouth plate with 1 preoral spine and 1–2 furrow spines; 2 furrow spines rarely on more than 5 mouth plates.

Material.—HOLOTYPE (USNM E28934): dry specimen (R = 20.9 mm, r = 6.4 mm), Sarasota Bay, Bradenton Beach, Florida, USA, 14 Jul 1981 (<1 m, oyster bed, 27°28.2'N, 82°42.1'W). PARATYPES: (USNM E28966), 16 dry specimens (R = 10.1 mm, r = 3.2 mm to R = 28.9 mm, r = 7.3 mm), same collection data as holotype; (USNM E28935), 8 specimens in ethanol (R = 12.2 mm, r = 4.2 mm to R = 17.0 mm, r = 5.4 mm), same location as holotype, 13 Jun 1977; (USNM E28936), 3 dry specimens (R = 16.5 mm, r = 4.9 mm to R = 21.0 mm, r = 5.5 mm), Sunshine Skyway Causeway, St. Petersburg, Florida, USA, 21 Jan 1978 (1 m, seagrass bed, 27°39.0'N, 82°40.5'W); (MCZ 4669), 12 specimens in ethanol (R = 14.8 mm, r = 4.5 mm to R = 24.9 mm, r = 7.3 mm), same collection data as USNM E28935; (YPM 10574), 13 specimens in ethanol (R = 14.2 mm, r = 5.2 mm to R = 20.4 mm, r = 5.8 mm), same collection data as USNM E28935; (DNR FSBC I 29872), 39 dry specimens (R = 6.8 mm, r = 2.3 mm to R = 22.4 mm, r = 5.4 mm), South Pass-a-Grille Channel, Cabbage Key, Tierra Verde, Florida, USA, 9 & 19 Apr 1975 (intertidal oyster bar, 27°40.3'N, 82°43.8'W); (BMNH 1982.11.26.1–10), 12 specimens in ethanol (R = 15.8 mm, r = 4.8 mm to R = 18.9 mm, r = 5.7 mm), same collection data as USNM E28935. Non-type material: (USNM E28967), 1 specimen in ethanol (R = 17.3 mm, r = 5.2 mm), St. Joseph Bay, Port St. Joe, Florida, USA, 31 Oct 1980 (seagrass bed, 29°47.9'N, 85°18.1'W) [originally, 6 specimens were examined].

Morphology.—Except where specifically mentioned, the following description is based on representative specimens from the type series. The body size is small, the largest specimen in the type-series having R = 28.9 mm. The 5 rays taper uniformly to somewhat rounded tips, with no inflation near the bases (Fig. 1A, B). The ratio of ray length (R = 20.9 mm) to disc radius (r = 6.4 mm) is 3.27 in the holotype. The body is covered by a thick skin, which obscures the small spines and the rest of the skeleton, even in dry specimens.

The 10 ossicles of the primary cirlet, including the madreporite, are distinct. In the trivium, each is connected to an adjacent member by an intercalary ossicle. Primary radials overlies the intercalary ossicles. Each primary radial connects distally and abradially with the first members of the paired adradial series of a ray. The primary interradials generally underlie the intercalary ossicles; but the madreporite has 2–4 basal projections (Fig. 1C) which directly underlie adjoining primary radials of the bivium, intercalary ossicles being absent. Each primary radial bears 1 spine in the holotype and 0–1 spine in the paratypes. Each primary interradial bears 0–1 spine in the holotype and 0–2 in the paratypes. The outer face of the madreporite is circular, flat, and slightly raised above the body wall. Madreporic gyri and sulci rarely have a radiating pattern; they usually form a meandering pattern with some gyri isolated from the periphery (Fig. 1C). Peripheral madreporic spinules are present and few (9 in the holotype, 2–16 in the paratypes); a few gyral spinules are sometimes present (3 in the holotype, 0–10

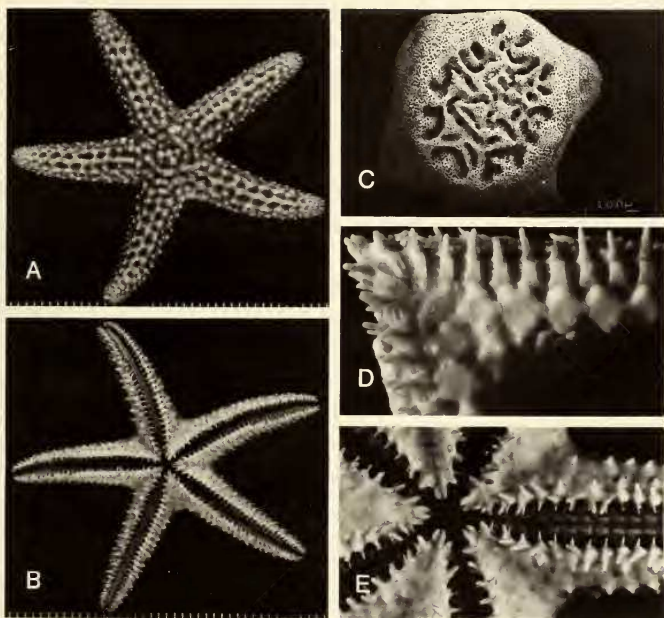


Fig. 1. *Echinaster graminicola*. A, Holotype, abactinal view; B, Holotype, actinal view; C, Madreporite, treated with alkali and prepared for scanning electron microscopy, specimen from type locality; D, Paratype (DNR FSBC I 29872), actinal view of a jaw and associated adambulacral and inferomarginal ossicles (with glassy tubercles), treated with alkali; E, Holotype, actinal view of disc and proximal part of a ray, showing oral and adambulacral spination.

in the paratypes). Spination of the madreporite seems to vary among populations. Within the primary cirlet are numerous periproctal plates, connected to form a reticulate complex; each plate sometimes bears a spine. The anus is surrounded by several spinules (5 in the holotype, 3–8 in paratypes), which are not attached to periproctal plates.

The series of primary and secondary ossicles of the outer wall of the rays are the carinals, adradials, dorsolaterals, superomarginals, intermarginals, inferomarginals, and adambulacrals (Fig. 2). Actinolaterals are absent. All ossicles except the dorsolaterals, intermarginals, and adambulacrals bear a central patch of glassy tubercles (Fig. 1D). Each ossicle of a series overlaps the next distal ossicle (distal imbrication), except as noted below. Papulae occur between all series. Papular areas are approximately equal in size to the surrounding ossicles in the proximal half of the ray. Papulae are most abundant (2–10) between the carinals and adradials. The carinals are triangular and bear 0–1 spine distally. Ossicles of the

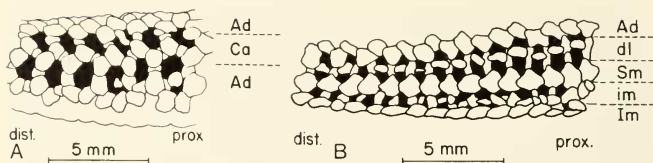


Fig. 2. *Echinaster graminicola*. Skeletal morphology of (A) abactinal and (B) lateral surfaces of the ray. Abbreviations: Ad, adradial ossicles; Ca, carinal ossicles; dist., distal end; dl, dorsolateral ossicles; Im, inferomarginal ossicles; im, intermarginal ossicles; prox., proximal end; Sm, supermarginal ossicles.

carinal row alternate left and right of the midline of the ray. Each carinal has one apex directed proximally, one distally, and one laterally. Intercalary plates often appear between successive carinals (Fig. 2A). The adradial ossicles are quadrilateral. They alternate left and right of the midline of the series, with one contacting a carinal ossicle and the next contacting a dorsolateral. Adradials bear 0-1 spine on the distal edge. Accessory ossicles connect the adradial and carinal ossicles. Adradials are connected to the supermarginals by 1, rarely 2, transversely oriented, cylindrical, dorsolateral ossicle. Each dorsolateral underlies an adradial at one end and a supermarginal at the other. The dorsolateral series sometimes includes a row of longitudinally oriented ossicles which overlie successive transverse ossicles (Fig. 2B). Proximal members of the dorsolateral series may bear 0-1 central spine. The series extends at least half the length of the ray.

The supermarginal ossicles are quadrilateral and bear 0-1 spine near the distal apex. No spines are found on the most proximal supermarginals. The ossicles form a linear, rather than alternating, row. The pattern of imbrication changes as the series progresses along the ray (Fig. 2B); ossicles near the disc have proximal imbrication; ossicles nearer the ray tip have distal imbrication; the point of change in pattern varies widely. An accessory plate (a transverse intermarginal ossicle) overlaps the adoral margin of each supermarginal. Near the ray tip, where dorsolateral and intermarginal ossicles are absent, the supermarginals overlap the adradials and underlies the inferomarginals. The intermarginal series, like the dorsolateral series, is composed of a row of cylindrical, transversely oriented ossicles (Fig. 2B). The intermarginals and dorsolaterals are similar in organization, spination, and length, with the two following exceptions: the aboral end of a transverse intermarginal overlies a supermarginal; the intermarginals form a crowded complex of flattened ossicles in the interradius. The inferomarginal ossicles are quadrilateral, and each bears 1, sometimes 0, spine distally. The most proximal inferomarginals bear no spines. The adoral apex of an inferomarginal overlaps 1-2 adambulacral ossicles. The inferomarginal series of adjacent rays meet behind the mouth plates, where there is usually a single inferomarginal ossicle in common (Fig. 1D).

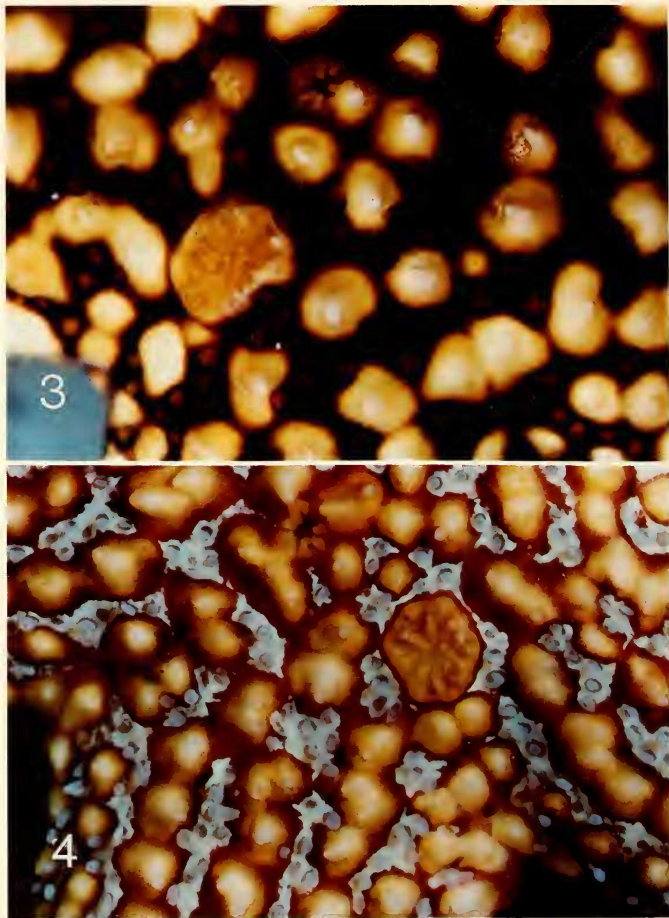
Adambulacrals have 1 furrow spine, 1 (sometimes 2) spine within the groove, and occasionally a subambulacral spine (Fig. 1E). When cleaned of skin, the furrow spine has a slightly flattened base; the column of the spine is cylindrical and narrower; the tip is enlarged, cylindrical, and provided all round with fine teeth;

the spine has a slight curvature toward the groove. Lying high within the ambulacral groove, there is a thin, small, compressed spine which curves toward the furrow spine. There is often an extra spine of intermediate size lying in the groove just above and slightly proximal to the furrow spine; it is more similar morphologically to the furrow spine; in some specimens, there appear to be 2 furrow spines, due to the projection of the extra spine out of the ambulacral groove. Subambulacral spines are single; they occur on few adambulacrals of specimens from Bradenton Beach and are more frequent in specimens from Cabbage Key and non-type material from St. Joseph Bay. Specimens usually have 2–3 spines per adambulacral; 4 spines is rare. Adjacent furrow spines are webbed together, as are a furrow spine and the 1 or 2 smaller spines which occur in the ambulacral groove.

Superambulacrals are present. Each connects an ambulacral and an infero-marginal. The circumoral ossicle and the distalmost ambulacrals do not have superambulacrals. The mouth plates bear 3–5 spines (Fig. 1E): 1 large preoral spine and 1–2 furrow spines, which are all webbed together; 1–2 small spines which occur within the groove; and, rarely, 1 suboral spine. Specimens with only 1 furrow spine on all mouth plates have been observed; specimens with 2 furrow spines on more than 5 mouth plates are rare.

Color.—Color terminology used here is based on Kelly and Judd (1955). The integument covering the ossicles ranges from deep orange yellow (ISCC-NBS number 69) to vivid orange yellow (no. 66), and the papular areas are blackish red (no. 21). The darker integument forms a continuous network surrounding islands of lighter integument (Fig. 3). This pattern gives the sea star a generally dark coloration with numerous light-colored knobs. The actinal surface is pale yellow (no. 89), with lines of dark brown (no. 59) where the few actinal papulae occur. Podia are vivid orange (no. 48). The distinctive coloration is lost upon preservation.

Ecological, reproductive, and physiological studies.—Possibly the first record of *E. graminicola* is that of Heilprin (1887), who found "*Echinaster* sp.?" in seagrass beds near Anclote Keys, Florida on 19 February 1886 during his cruise on the schooner "*Rambler*." Unfortunately, specimens were apparently not deposited in collections of the Wagner Free Institute of Science (J. Graham, pers. comm.). Definite records of *E. graminicola* in the literature begin with Ferguson's (1966) pharmacological study of tonal changes in pyloric caeca. Ferguson (1967) recognized early in his work that unresolved taxonomic problems with the genus required specification of the source of his material, and his practice of including cautionary footnotes fortunately was adopted by other investigators in the Tampa Bay area. *Echinaster graminicola* was the subject of Ferguson's (1967, 1968, 1970, 1975a, 1980a, b, 1982) several papers on the uptake and translocation of amino acids and other dissolved organic matter by sea stars. Ferguson (1974, 1975a, b, 1976) also studied the annual reproductive cycle and the changes in chemical composition of body components associated with the cycle. Atwood (1973a) described embryogenesis, larvigeneration, and early post-metamorphic growth. Turner (1977) described the use of yolk during development, and Turner and Lawrence (1979) characterized the shape, volume, and biochemical composition of the egg. Watts *et al.* (1982, 1983) described the effects of salinity and temperature combinations on morphogenesis and growth. More general studies of the life history



Figs. 3-4. 3, *Echinaster graminicola*. Abactinal view of part of disc of live animal from type-locality. 4, *Echinaster spinulosus*. Abactinal view of part of disc of live animal from Mullet Key, St. Petersburg, Florida (2m, sandy bottom).

and population ecology of *E. graminicola* were done by Scheibling (1982) and Scheibling and Lawrence (1982). Atwood and Simon (1973) localized and histochemically analyzed neurosecretory granules in various organs. Atwood (1973b) presented evidence that the granules were gonad stimulating substance (GSS) by histological examination of radial nerves before, during, and after spawning; Atwood (1973c) assayed for the presence of GSS in several organs. Further work in reproductive endocrinology was done by Turner (1976). Campbell's (1978) study of ossicle and skeletal morphology led to the discovery by Turner and Campbell (1981) that the species was not *E. modestus*. It is possible that *E. (Othilia) modestus* used by Blake (1978, 1980) for comparative studies of ossicle and skeletal morphology were *E. graminicola*, but we have not examined his specimens.

Based on the studies mentioned above, the following profile of *E. graminicola* emerges. Animals have an annual reproductive cycle, spawning in April and May apparently under influence of the same hormonal system found in other asteroids. The egg is an orange, oblate spheroid measuring 0.84–0.88 mm in diameter and about 0.260 ml in volume. The egg has a lipid-to-protein ratio close to 1:1 and has a very high density of organic matter. The egg is adherent to seagrass blades and other substrata and hatches within 2 days into a demersal lecithotrophic larva. Larvae are quite tolerant of changes in temperature, less tolerant of changes in salinity. The mouth opens at 14 days post-fertilization after the loss of 20–25% of the original egg organic weight. Juveniles require about 2 yr to reach sexual maturity, at a size of R = 11–12 mm. During this period of growth, they remain in seagrass (*Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*) and oyster beds at shallow depths, feeding on epibiota and facultatively absorbing dissolved organic matter released by the sessile organisms that form the substratum.

Type-locality.—Sarasota Bay, Bradenton Beach, Anna Maria Key, Florida, USA (27°28.2'N, 82°42.1'W), <1 m depth, along bulkhead, on oysters and pilings.

Distribution.—*Echinaster graminicola* has been collected extensively in the Tampa Bay area: from oyster beds, bulkheads, and pilings in Sarasota Bay; from *T. testudinum* beds along the Sunshine Skyway Causeway; from *T. testudinum* beds, oyster beds, pier pilings, and cement bulkheads around Mullet, Madelaine, and Cabbage keys. The species has been found at Seahorse Key, Cedar Keys, Florida in *S. filiforme* beds. Specimens from *T. testudinum* beds in St. Joseph Bay, Florida have been identified by us as *E. graminicola*. The maximum depth at which the species has been collected is 2 m.

Relationships.—Among the several species of western Atlantic *Echinaster*, *E. graminicola* is most similar to *E. spinulosus*, with which it has been repeatedly confused. The discussion below and accompanying Table 1 are given to emphasize the differences between the two species.

Live specimens of *E. graminicola* and *E. spinulosus* can be readily distinguished by color (Figs. 3, 4). The integument covering ossicles of the aboral surface of *E. spinulosus* is deep reddish orange (ISCC-NBS number 36) to deep orange yellow (no. 69), and the papular areas are bluish white (no. 189). The papular areas are numerous but small, and the animal overall looks "orange." On the adoral surface, the sea star is pale yellow (no. 89), and no areas of bluish white integument occur.

Preserved specimens of the two species are distinguished by few differences in

spination and morphology. Some of the differences listed in Table 1 might reflect a neotenic condition in *Echinaster graminicola*, but the differences are not always related to body size of specimens we examined. *Echinaster graminicola* is generally less spiny than *E. spinulosus*, but it is difficult to identify individual specimens. Even the adambulacral armature of one species is easily derivable from the other: in *E. graminicola*, the 3 spines are in a slightly curved vertical row; in *E. spinulosus*, the "middle" spine is close enough to the distal furrow spine in position and morphology to be considered a second furrow spine. Oral armature, on the other hand, seems to be a reliable character for identification of individual specimens.

Many differences other than adult morphology of the two species have been found by other authors (Table 1). The species differ especially in reproduction, development, biochemistry, physiology, microhabitat, and general size. Scheibling (1982) and Watts *et al.* (1982) give evidence of a genetic basis for some of these differences.

Echinaster graminicola and *E. spinulosus* are easily distinguished from the rarer and deeper-water *E. modestus*, which has an actinolateral series, more complex organization of dorsolaterals, predominance of proximal imbrication, shorter and more compact series of intermarginals, poorly developed patches of glassy tubercles, and spinier adambulacrals and mouth plates (Turner and Campbell 1981). They are similarly distinct from specimens on which Downey (1973) and Tortonese and Downey (1977) based their taxonomic treatment of *Verrillaster* Downey, 1973. On the other hand, *E. graminicola* and *E. spinulosus* are allied to *E. sentus*, which also lacks actinolaterals and has well-developed patches of glassy tubercles.

Etymology.—*graminicola*, from the Latin *gramen*, grass, and *colo*, to dwell; referring to the frequent occurrence of this species in seagrass beds, used as a noun in apposition.

Discussion.—*Echinaster graminicola* and *E. spinulosus* are sibling species (sensu Kohn and Orians 1962; Mayr 1969). They are sympatric and morphologically similar, with a high degree of niche specialization. They have been recognized as distinct forms for at least 16 years (Ferguson 1967) on the basis of ecological and other non-morphological data. The two species were hybridized by Scheibling (1982) and Watts *et al.* (1982) but are isolated by different spawning times and microhabitats. Only recently (Campbell 1978; Campbell and Turner 1979) was a morphological basis for their distinction as species found.

The sea star family Echinasteridae Verrill, 1867 is a problematical group that includes *Echinaster*, *Henricia*, and other genera which have undergone repeated taxonomic revision (Fisher 1919; Rasmussen 1965; Tortonese and Downey 1977). Grainger (1966) wrote that species of *Henricia* are "chronic sources of trouble to students of the group;" and Downey (1973) described the genus *Echinaster* as "the most confusing one [among the Asteroidea] occurring in the tropical and subtropical Atlantic." One reason for the taxonomic problems is the high degree of intraspecific morphological variability. The presence of non-morphological variability within and among other western Atlantic populations of *Echinaster* (Tuttle and Lindahl 1980), in addition to the present case, suggests to us that problems in the Echinasteridae might be due to the existence of numerous sibling species.

Table 1.—Contrasting characteristics of *Echinaster graminicola* and *E. spinulosus*. References: 1, this report and authors' unpublished observations; 2, Atwood (1973a); 3, Turner and Lawrence (1979); 4, Scheibling and Lawrence (1982); 5, Watts *et al.* (1982); 6, Scheibling (1982).

Character	<i>Echinaster graminicola</i>	<i>Echinaster spinulosus</i>	Ref.
Color			
Papular areas	Blackish red	Bluish white	1
General pattern	Dark red with numerous yellow knobs	Orange	1
Meristics and morphology			
Aboral disc spines	Tapered, subacute	Cylindrical, obtuse	1
Mouth plate spines	2-3	3-4	1
Ray spines	0-1	1-2	1
Furrow spines	1	2	1
Intercalary carinals	Usually present	Usually absent	1
Madreporic gyri	Meandering	Radiating	1
Gyral spines	0-10	3-34*	1
Peripheral spines	2-16	12-37*	1
Egg			
Color	Orange	Brown	2, 3
Shape	Oblate spheroid	Prolate spheroid	3
Diameter	.84-.88 mm	1.0-1.3 mm	2
Volume	.258 ml	.199 ml	3
Lipid : protein ratio	1:1	5:2	3
Organic density	595 $\mu\text{g}/\text{ml}$	439 $\mu\text{g}/\text{ml}$	3
Buoyancy upon spawning	Sinks	Floats	2, 3
Reproduction and growth			
Spawning	April-May	Late May-June	4
Larva	Demersal	Pelagic	2
Larval temperature tolerance	Greater	Less	5
Growth rate 1st yr	10 mm/yr	22 mm/yr	6
Maturity	Later age, smaller size	Earlier age, larger size	4
Reproductive effort	Higher	Lower	4
Fecundity	1 \times	3-5 \times	4
Reproductive output	Lower	Higher	4
Caloric investment/egg	1.7 \times	1 \times	4
General size	Smaller	Larger	1, 6
Ecology			
Habitat	Shallow; seagrass and oyster beds, pilings, bulkheads	Deep; bare sand, pilings, bulkheads	1, 6
Diet**	Sessile epifauna	Sessile, sedentary epifauna; scavenging	1, 6

* Based only on 5 cotypes, YPM 1771.

** Dietary differences are probably greater, based on analysis of fatty-acid composition of adults (Ferguson 1976).

Blake (1973) found that the morphology of individual ossicles of the primary skeleton was sufficiently consistent intraspecifically to be useful in taxonomic studies of four Recent asteroid families. The detailed examination of individual primary ossicles was, however, of limited value in the present case (Campbell

1978). In closely related species of *Echinaster*, evolution has probably occurred faster in the morphology of the secondary skeleton (Schuchert 1915) than in the morphology of primary ossicles; and the subtle differences might not be discovered until *Echinaster* populations are better known ecologically.

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Note added in proof:

Echinaster graminicolus, nomen nudum, has inadvertently appeared in Ferguson (1984).

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